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Morphological Caste Differences in the Neotropical Swarm-founding Polistine Wasps IV: *Pseudopolybia vespiceps*, with Preliminary Considerations on the Role of Intermediate Females in the Social Organization of the Epiponini (Hymenoptera, Vespidae)

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Abstract.—The measurements of 22 body parts and counts of hamulus number for 300 wasps from a colony of *Pseudopolybia vespiceps* evidenced the occurrence of three types of females, i.e., queens (inseminated egg-layers), workers (uninseminated, non egg-layers), and intermediates (with well developed ovaries but uninseminated). Caste-linked aspects in this species are, thus, complex. Queens (Q) and workers (W) differed in only two characters (basal width of the second gastral tergite and hamulus number) (Bonferroni-test, $p < 0.05$), so, these castes can be considered as morphometrically similar. On the other hand, intermediates (I) were significantly larger than queens and workers in some body parts ($p < 0.05$). Canonical discriminant analysis revealed that Mahalanobis distances (D^2) between Q/W, Q/I and I/W were very small, 0.99, 1.51 and 1.12, respectively. In spite of this, color patterns of head and gastral parts separate queens and workers very well. In such aspects intermediates combine queen-worker similarities.

In social insects, approaches related to caste differences constitute a form of evidencing queen-worker specializations. To study the diversity of such aspects, the swarm-founding polistine wasps are very helpful because the castal differences so far known can be arranged along a spectrum ranging from taxa in which queens and workers are externally similar, to others with fairly distinct caste attributes. Despite occurence of transitional steps (e.g. *Protopolybia exigua* cf. Simões 1977; Noll et al. 1996), our previous serial papers showed two contrasting cases: queen dwarfism, as promoted by the prevalence of smaller body parts in queens relatively to workers (*Apoica flavissima* and *Polybia dimidiata*: Shima et al. 1994 and Shima et al. 1996a, respectively), and queens larger than workers in most of the morphological characters (*Protonectarina sylveirae*: Shima et al., 1996b). Moreover, the taxa under such opposite trends showed also different color patterns allied to conspicuous external morphological peculiarities. However, the most pronounced dimorphism among polistine wasps has been found in some *Agelaia* (*Stelopolybia* auct.) species, such as, *A. flavipennis* (Evans & West-Eberhard 1970); *A. areata* (Jeanne and Fagen 1974; Jeanne 1980 1991), *A. pallipes* and *A. multipicta* (Noll et al. 1997) and *A. vicina* (Sakagami et al. 1996; Baio et al. in press).

The genus *Pseudopolybia* is poorly known. Indeed, only some details on nest architecture and fragmentary morphometric features had so far been reported by Richards

(1978, and references therein), before the recent paper on *Ps. difficilis* (Jeanne 1996). Contrary to those taxa previously studied in our serial papers, *Ps. vespiceps* shows no clear-cut morphological caste dimorphism. In addition, *Ps. vespiceps* evidenced the occurrence of intermediate females which are characterized by the combination of well developed ovaries and the absence of insemination (Richards & Richards 1951). Although the bionomic importance of such females remains largely speculative, their significance in the colonial socio-economics is apparently relevant because Naumann (1970), Simões (1977) and M. V. Baio (unpubl.) have found out that intermediates in *Protopolybia acutiscutis* (cited as *P. pumila*) and *P. exigua exigua*, frequently laid eggs which were primarily eaten by the layer herself. Based on the morphometric analysis adopted in our serial work, this paper deals with caste differences and related aspects in *Pseudopolybia vespiceps testacea* Ducke.

MATERIAL AND METHODS

A mature colony (A) of *Pseudopolybia vespiceps testacea*, from which a small number of individuals escaped during collection, was taken on 20 January 1975 in Ribeirão Preto, São Paulo State, southeastern Brazil. The 603 collected wasps, all of which were females, were fixed in Dietrich's solution and then kept in 70% ethanol until dissection. From this sample, 300 wasps were randomly chosen for examination. In order to detect caste differences the following 22 external body parts were measured and the number of hamuli was counted for each specimen under a binocular microscope: (1) head width (HW), (2) head length (HL), (3) and (4) maximum and minimum interorbital distances (IDx, IDm), respectively, (5) gena width (GW), (6) eye width (EW), (7) pronotal width (PW), (8), (9) length and width of mesoscutum (MSL and MSW), respectively, (10) mesoscutellar length (MTL), (11) metanotal length (MNL), (12) mesosomal height (MSH), (13) alitrunk length (AL), (14) propodeum length (PL), (15) length of gastral tergite I (T_1L), (16), (17) basal and apical heights of T_1 (T_1BH, T_1AH), respectively, (18), (19) basal and apical widths of gastral tergite II (T_2BW, T_2AW), respectively, (20), (21) length and height of T_2 (T_2L, T_2H), respectively, and (22) partial length of the forewing (WL) (See Fig. 2 in Shima et al. 1994). In addition, color patterns and other morphological peculiarities were examined. The numerical data were statistically analyzed in relation to ovarian and spermathecal conditions.

The statistical analyses including the canonical discriminant analysis (CDA: Rao 1973) and Mahalanobis's distances (Anderson 1968) through CDA were performed with the SAS Program Package at the Computer Center of Kyoto University. Afterwards, a second colony (B) was collected on February 3, 1995 in Pedregulho, São Paulo State. The illustrations (Fig. 1A, B, C, and D) pertain to this colony.

RESULTS

Nest architecture and colony composition.—Both nests (A,B) were found in shady places at about 3 m high aboveground and both were hung from terminal small branches, of which ramifications pierced the outer envelope at upper parts, but not the combs. In shape (ellipsoidal), size (17.0 cm high, 12 cm ø) and number of combs (8 and 7, respectively) both nests were very similar and so these features may represent the size reached by the mature colonies of *Ps. vespiceps* (Fig. 1). The multilayered greyish envelope covered combs entirely. It had several, sometimes indistinct, vertical rows formed by several pulp additions during construction (Fig. 1A–D). The nest top, which incorporated some twigs, was somewhat spongy, but latterally the envelope was formed by two to four layers of delicate and loose sheets (Fig. 1B). The nest entrance, which was large and devoid of special structures (Fig. 1C), was located at the lowermost part of

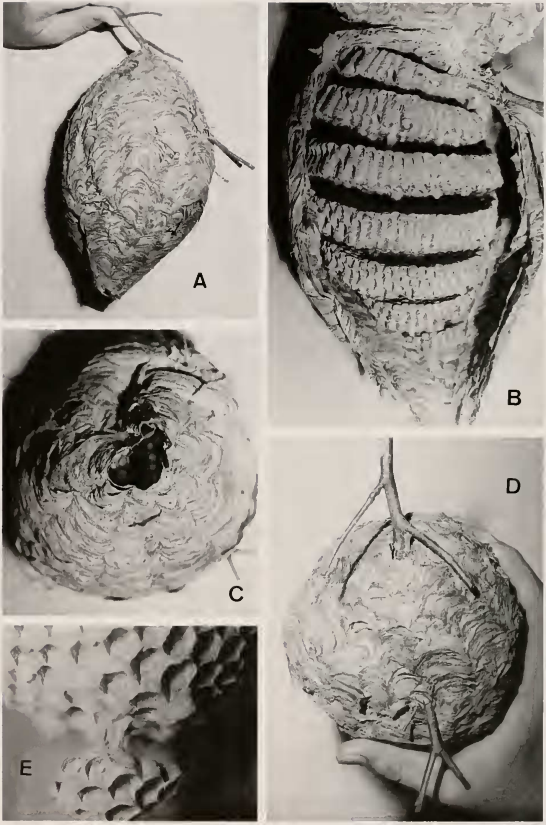

Fig. 1. Nest of *Pseudopolybia vespiceps*: A—held in the position as in nature; B—with the outer envelope removed partially; C—oriented as to exhibit an enlarged entrance and a part of the lower comb; D—seen from the top; E—lowermost combs and pedicel. A–D, nest 2; E, nest 1.

the nest. Each comb was hung below the other by a single centrally located paper pillar (1.0 cm long, 1.0 cm wide; Fig. 1E). The only exception was the uppermost comb which was attached to the substrate, a twig, by a row of 4 or 5 thin pillars. The first comb was solely supported by these pillars and, therefore, all combs hung from the upper one independently of the envelope. As recorded by Richards (1978) the general plan of *Pseudopolybia* nests is similar to *Vespula norwegica* of subfamily Vespinae. As stated above, colony A used in this study had 603 adult females (118 queens, 396 workers, 89 intermediates) and no males. The queen ratio (total queen number/total female number) was 0.196. Eight combs had 729 eggs, 584 larvae, 586 cocoons and 287 empty cells.

Ovarian development and insemination.—In the analyzed sample four types of ovary development were recognized (Fig. 2): type A (short ovarioles): A_1, thread-like with no sign of development ($n = 60$), A_2, slightly developed ($n = 74$) and A_3 ($n = 10$), more developed than A_2; type B (in developmental stages similar to type A, but with longer ovarioles); B_1, B_2, B_3 ($n = 13$, 33 and 7, respectively); type C ($n = 44$), moderately developed with a few (1 to 3) mature oocytes (mean 1.9, $n = 85$) and type D ($n = 59$), well developed with an average of 3.7 mature oocytes (range 1 to 7), $n = 176$. Since insemination was detected exclusively in females with type D ovaries, only these females are regarded as queens. All the others females were uninseminated, and those with type C (developed) ovaries were regarded as intermediates (sensu Richards and Richards 1951; Richards 1971). Conversely, females with A and B ovary types constitute the cohort of workers. Although measurements were not made, mature oocytes in the intermediates were clearly smaller than those in queens.

Ovariole length, wing-wear patterns and relative amount of fat tissue.—Mean ovariole length (MOL) was longer in queens (8.52 ± 0.46 mm, $n = 46$), followed by B typed workers (7.63 ± 0.38 mm), intermediates (6.95 ± 0.57 mm), and smallest in A typed workers (6.69 ± 0.39 mm). These differences were statistically significant (ANOVA, $p < 0.01$, $F = 0.242$). Another interesting tendency was found connecting ovary development and amount of fat tissue. Indeed, individuals showing progressive kinds of ovary development presented also larger amounts of fat tissue. The culmination of such tendency was found in D typed females (queens) which showed higher amounts of fat reserve (grade IV, cf. captions in Fig. 3). Most uninseminated females (type A ovaries) had shorter ovarioles relative to the B typed ones, and both had little (I) or moderate (II) amounts of fat tissue. But, some uninseminated callow females, which were recognized by their pale and soft cuticule, had larger amounts of fat tissues also (grade IV). In this case, it seems that the mere presence of larger amounts of fat tissue is not conclusively connected to further queenhood. Indeed, extensive dissections in representatives of taxa with clearcut caste differences suggest that callow stages of both castes invariably present conspicuous fat amounts (Noll unpubl.).

Figure 3 shows the relations between ovary development and wing-wear in the different kinds of Ps. vespiceps females. Grades of wing-wear showed relationship to the relative amount of fat tissues. Most analyzed females, including all queens, had fresh wings (pattern 0), while some workers and intermediates showed consistent wing-wear (patterns 1–3, Fig. 3). Wing-wear may indicate relative age progression and flight activities. The fact that all queens had fresh wings suggest their absence in extranidal tasks.

Morphometrics and hamulus number.—Differences of mean values of 24 characters measured or counted were tested in workers, queens and intermediates by Bonferroni-test (Table 1). Between workers and queens, significant differences were

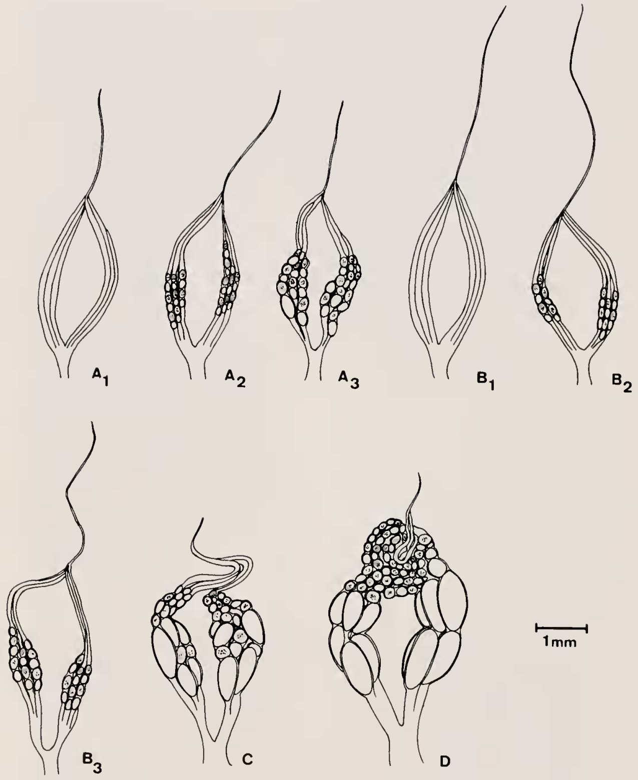

Fig. 2. Grades of ovarian development in *Pseudopolybia vespiceps*. Type A: short ovariole type. A_1-thread-like; A_2 and A_3-showing initial development of the oocytes); Type B: long ovaries type. B_1-thread-like as in A_1; B2 and B3-comparable to A_2 and A_3, respectively; Type C: moderately developed with a few mature oocytes; and Type D: well developed and bearing many mature oocytes. Other explanations, in the text.

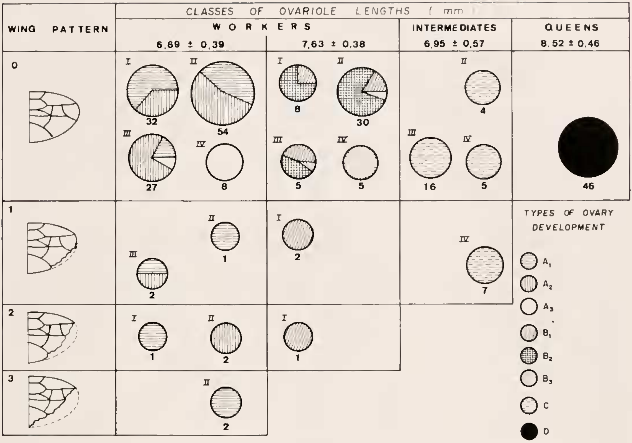

Fig. 3. Relationships between wing patterns (0 = fresh; 1–3 = worn in ascending order) and relative amounts of fat tissue (I = few; II = moderate; III = abundant; IV = much abundant). Number of individuals for each class of fat tissue is expressed by the size of circle, in which numbers of individuals of different ovarian types are shown.

detected only in T_2BW, being larger in workers, and NH, larger in queens ($p < 0.05$). Between queens and intermediates, means of five characters, i.e., HW and HL, Idx, T_2L, T_2BW and NH differed ($p < 0.05$). Values of all but one character (NH) were larger in the intermediates. Between intermediates and workers, differences were detected in four characters, HW, IDx, MSW and T_2H ($p < 0.05$), all of which were larger in intermediates. No significant difference was detected in AL, regarded as a reference length for comparing sizes, among the three classes of females. This implies that size differences are so small that virtually no size polymorphism exists in this species. But, it is noteworthy that the intermediates are larger in some characters than workers and even queens.

The results of the canonical discriminant analysis (CDA) based on 23 characters also show the absence of clear dimorphism between inseminated egg-layers (queens) and uninseminated non-egg-layers (workers) (Fig. 4). Queens and workers were plotted against scales of the CAN_1 and CAN_2 variables between −3.0 and 3.0 and −2.5 and 2.5, respectively. The distribution pattern of the intermediates was very peculiar because their plots showed a vertical distribution at the right side in the scatter diagram. Only one queen and one worker presented higher CAN_2 values than intermediates.

To calculate the CAN_1 and CAN_2 values the following equations were used (see table 1): $CAN_1 = -0.47\,(HW - 3.79) + 5.24\,(HL - 3.04) - 0.36\,(Idx - 3.17) - 5.13\,(IDm - 1.81) + 0.53\,(GW - 0.94) - 1.98$

Table 1. Means and CAN_1 and CAN_2 values for 23 characters examined.

Characters	Means (mm) ± SD			CAN_1 values		CAN_2 values	
	Queens	Workers	Intermediates	Standardized	Raw	Standardized	Raw
HEAD							
HW**,'	3.78 ± 0.07	3.82 ± 0.06	3.78 ± 0.08	−0.04	−0.47	0.67	8.86
HL**	3.02 ± 0.09	3.07 ± 0.08	3.04 ± 0.08	0.45	5.24	−0.41	−4.81
IDx*'	3.17 ± 0.06	3.20 ± 0.08	3.17 ± 0.08	0.03	−0.36	−0.11	−1.51
IDm	1.81 ± 0.04	1.83 ± 0.05	1.81 ± 0.05	−0.24	−5.13	−0.24	−5.19
GW	0.94 ± 0.06	0.95 ± 0.05	0.94 ± 0.06	−0.03	0.53	0.09	1.53
EW	0.88 ± 0.06	0.88 ± 0.04	0.88 ± 0.06	−0.11	−1.98	−0.12	−2.30
MESOSOMA							
MSL	2.48 ± 0.06	2.49 ± 0.07	2.48 ± 0.07	−0.01	−0.12	0.22	3.36
MSW'	2.50 ± 0.06	2.53 ± 0.06	2.50 ± 0.07	0.13	1.86	0.16	2.30
PW	3.20 ± 0.08	3.24 ± 0.07	3.21 ± 0.09	−0.09	1.02	0.15	1.75
MTL	1.14 ± 0.04	1.15 ± 0.04	1.13 ± 0.04	−0.10	−2.35	0.25	6.10
MNL	0.66 ± 0.05	0.66 ± 0.05	0.65 ± 0.05	−0.30	−5.88	0.29	5.67
MSH	3.55 ± 0.13	3.57 ± 0.13	3.53 ± 0.14	−0.02	−0.14	0.19	1.41
AL	4.93 ± 0.12	4.95 ± 0.11	4.92 ± 0.13	−0.18	−1.47	0.05	0.40
METASOMA							
PL	1.44 ± 0.08	1.47 ± 0.08	1.44 ± 0.08	0.34	4.14	0.07	0.82
T_1L	2.10 ± 0.08	2.14 ± 0.08	2.12 ± 0.10	0.05	0.49	−0.07	−0.80
T_1BH	0.87 ± 0.09	0.86 ± 0.07	0.86 ± 0.08	−0.34	−4.12	−0.13	−1.58
T_1AH	1.53 ± 0.09	1.56 ± 0.10	1.55 ± 0.10	0.17	1.71	−0.15	−1.53
T_2L**	2.90 ± 0.13	2.97 ± 0.10	2.92 ± 0.13	0.32	2.44	−0.23	−1.78
T_2BW*,**	2.33 ± 0.11	2.42 ± 0.13	2.38 ± 0.14	0.56	4.21	−0.22	−1.62
T_2AW	3.68 ± 0.12	3.70 ± 0.15	3.67 ± 0.15	−0.31	−2.17	0.04	0.29
T_2H'	3.19 ± 0.16	3.26 ± 0.14	3.14 ± 0.16	0.34	2.11	0.74	4.54
WING							
WL	5.09 ± 0.10	5.13 ± 0.10	5.10 ± 0.13	0.02	0.20	−0.42	−3.43
NH*,**	9.59 ± 0.89	9.07 ± 0.73	9.26 ± 0.84	−0.57	−0.57	0.04	0.04

Full names of characters are explained in the text (see Material and Methods).
*,**,' Mean significant differences between queens and workers, queens and intermediates and intermediates and workers, respectively (Bonferroni t-test, $p < 0.05$).

(EW − 0.88) − 0.12 (MSL − 2.48) + 1.86 (MSW − 2.51) + 1.02 (PW − 3.21) − 2.35 (MTL − 1.14) − 5.88 (MNL − 0.66) − 0.14 (MSH − 3.54) − 1.47 (AL − 4.92) + 4.14 (PL − 1.45) + 0.49 (T1L − 2.12) − 4.12 (T1BH − 0.86) + 1.71 (T1AH − 1.55) + 2.44 (T_2L − 2.92) + 4.21 (T_2BW −2.37) − 2.17 (T_2AW− 3.68) + 2.11 (T_2H − 3.17) + 0.20 (WL − 5.10) − 0.67 (NH − 9.30)

CAN2 = 8.86 (HW − 3.79) − 4.81 (HL − 3.04) − 1.51 (IDx − 3.17) − 5.19 (IDm − 1.81) + 1.53 (GW − 0.94) − 2.30 (EW − 0.88) + 3.36 (MSL − 2.48) + 2.30 (MSW − 2.51) + 1.75 (PW − 3.21) + 6.10 (MTL − 1.14) + 5.67 (MNL − 0.66) + 1.41 (MSH − 3.54) + 0.40 (AL − 4.92) + 0.82 (PL − 1.45) − 0.80 (T1L − 2.12) − 1.58 (T1BH − 0.86) − 1.53 (T1AH − 1.55) − 1.78 (T2L − 2.92) − 1.62 (T2BW − 2.37) + 0.29 (T2AW − 3.68) + 4.54 (T2H − 3.17) − 3.43 (WL − 5.10) + 0.04 (NH − 9.30)

The most important variable to determine CAN1 was MNL. Some other variables, such as HL, IDm, T_2BW and T_1BH were also important. The most important variable to determine CAN_2 was HW. Mahalanobis's distances (D^2) between queens and workers, queens and intermediates and intermediates and workers were 0.99, 1.51 and 1.12, respectively, showing that, as

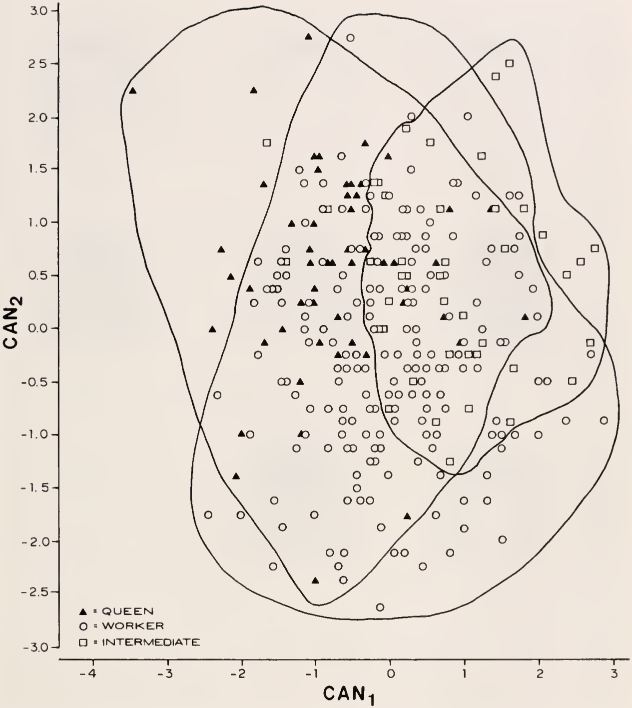

Fig. 4. Discrimination among queens, workers and intermediates of *Pseudopolybia vespiceps* by the canonical discriminant analysis based on 23 characters. Other explanations in the text.

expected from the result of basic statistics, queens are morphologically more similar to workers than to intermediates.

Aspects related to color patterns and external morphology.—Differences that were more conspicuous than morphometric characters were found in head, mesosoma and metasoma.

Head (Fig. 5): Workers heads are of various shapes. Despite sequentially continuous, these characteristics can be grouped into three major types, i.e., flat, ovate and pointed types (types I–III), and four color patterns (A_1 to A_4). A tendency was detected and it shows that the coloration of the flat head type is lighter than in the

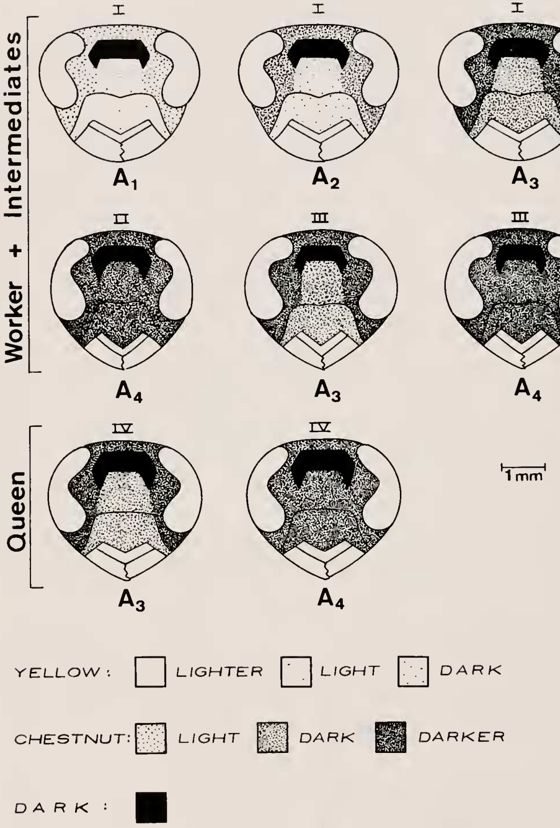

Fig. 5. Color patterns and shapes of head in queens, workers and intermediates of *Pseudopolybia vespiceps*. Color: A_1 to A_4; Shape: I. flattened; II. ovate; III. pointed; IV. ovate but more enlarged apically.

ovate and pointed head types. On the other hand, ovate head (type IV) characterizes the queens in which two color patterns (A_3, A_4) appear, and these are very similar to the workers darkest forms.

Mesosoma (Fig. 6): Workers present six mesosomal color forms ranging from light (B_1) to dark (B_6). Mesoscutellum of each type presents (or not, see type a, B_1) a pair of dark spots which vary in size and form (separated circles, ellipsoids partly fused) (e.g., types b–e, B_1). Except for type B_6 there are no double transverse bands on the mesoscutellum. On the other hand, queens present only one color form (B_7), but as workers, they present various spot types (a–e) on the mesoscutellum. In addition, a pair of arched transverse bands occur near the basal and apical margins of the mesoscutellum (apical bands are often lighter in color and more vestigial than basal ones). Such bands are seen through the transparent cuticule (Fig. 6, B_6 b–d, B_7 a–e). Despite color patterns overlap among the diverse types of females, mesoscutellar bands easily discriminated queens from workers. In intermediates, the patterns of the head and thorax were similar to workers including a tendency for the flat type of head (n = 30) and lighter colors (A_1, n = 9; A_2, n = 7; A_3, n = 14). Indeed, only one intermediate presented A_4 II pattern which is similar to queens. From 16 color patterns of the worker's thorax, 12 were similar in intermediates with higher frequency of B_1 b (12); B_1 e (7), B_5 e (8). Conversely, only B_1 a,c; B_3 b and B_4 e were not observed in such females.

Metasoma (Fig. 7): Three major color forms (G_1–G_3) occur, and each form has three to five color variations on T2 (C_1–C_{11}). Queens and intermediates present lighter gastral patterns (G_1 and C_1–C_4), among which C_3 is the most frequent (n = 28). Workers have darker gasters (G_2 and G_3, and C_2, C_5–C_{11}), among which C_5 and C_6 are the most frequent (n = 80 and 77, respectively). In intermediates, six forms occur (G_1, C_1–C_4, and G_2, C_5, with the highest frequency in C_2 (n = 18) and C_3 (n = 14). Although form C_2 is shared by all kinds of females, queens generally present lighter and enlarged gasters than workers.

DISCUSSION

Although caste differentiation in social wasps is most conspicuous in the Vespinae, especially *Vespula* (Blackith 1958; Spradbery 1972), certain swarm-founding polistine wasps have also evolved distinct size dimorphism. Such a fact was clearly stated long ago by von Ihering (1903), who described remarkable morphological caste differences in *Agelaia vicina*, but his results have been overlooked by modern specialists in spite of its citation by Richards and Richards (1951). Indeed, additional records on quite conspicuous caste differentiation in the Polistinae, analyzed either qualitatively and/or quantitatively by statistical methods, appeared only recently. Genera and species examined are: New World: *Agelaia flavipennis* (Evans and West-Eberhard 1970); *A. areata* (Jeanne and Fagen 1974); *Polybia emaciata* (Hebling and Letízio 1973); *Polybia dimidiata* (Maule-Rodrigues and Santos 1974; Shima et al. 1996a); *Apoica flavissima* (Shima et al. 1994); *A. pallens* (Jeanne et al. 1995); *Protonectarina sylveirae* (Shima et al. 1996b), *Pseudopolybia difficilis* (Jeanne 1996), and *Epipona guerini* (Hunt et al. 1996), and Old World genera: *Ropalidia montana* (Yamane et al. 1983); *R. bambusae* and *R. leopardi* (Kojima and Kojima 1994); *Polybioides tabidus* (Richards 1969; Turillazi et al. 1994), etc. In the Polistinae, according to Richards (1978) at least three patterns of caste differentiation are found: 1) Conspicuous size and allometric differences present, with queens larger than workers in the absence of intermediates (*Agelaia* spp: *A. areata*, Jeanne and Fagen 1974; *A. pallipes* and *A. multipicta,* Noll et al. 1997; *A. vicina,* Sakagami et al. 1996; *Protonectarina sylveirae,* Shima et al. 1996b; *Epipona guerini,* Hunt et al. 1996); 2) Conspicuous dimorphism present, with queens smaller than workers in most char-

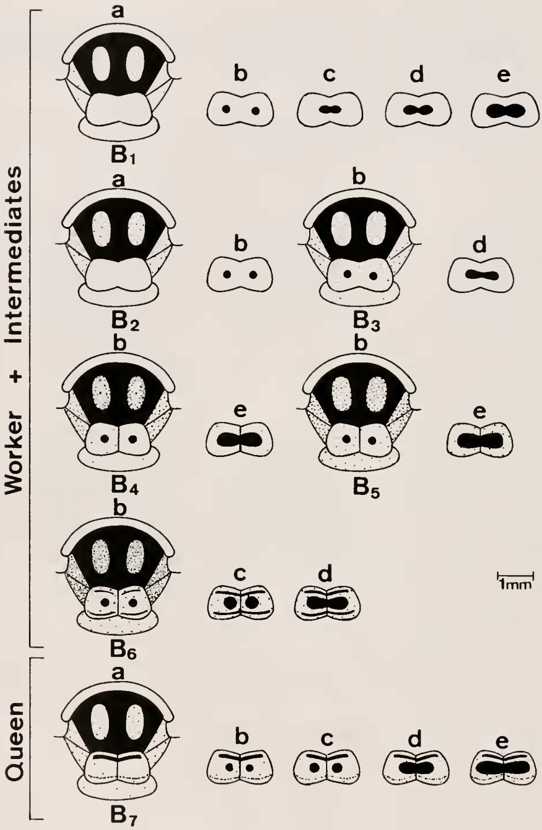

Fig. 6. Color patterns (B_1 to B_7) and mesoscutellar spots (a–e) in queens, workers and intermediates of *Pseudopolybia vespiceps*.

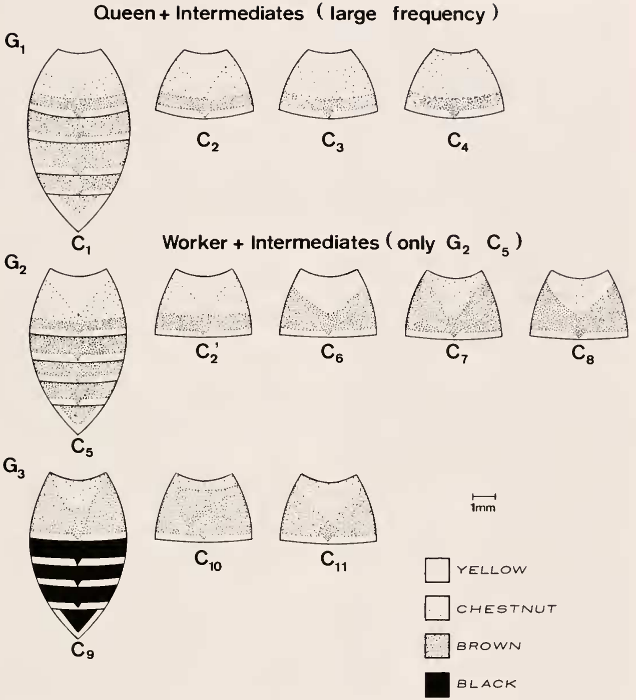

Fig. 7. Color patterns (G_1–G_3) in the gastral parts (C_1–C_{11}) of queens, workers and intermediates of *Pseudopolybia vespiceps*.

acters and intermediates absent (*Apoica flavissima*, Shima et al. 1994; *Polybia dimidiata*, Shima et al. 1996a); 3) Morphological differences slight or indistinct, and intermediates present (*Parachartergus smithii*, Mateus et al. 1997; *Protopolybia exigua*, Noll et al. 1996; and *Pseudopolybia vespiceps*, present work). However, in some groups, queens are significantly smaller than workers in some characters and larger in others (*Apoica pallens*, Jeanne et al. 1995; *Pseudopolybia difficilis*, Jeanne, 1996), and according to Jeanne et al. (1995) this is considered as non-size-based caste dimorphism probably due to a reprogrammation in growth parameters (Wheeler, 1991).

Differently from *Pseudopolybia difficilis*

(Jeanne 1996), *P. vespiceps* presented slight caste dimorphism between queens and workers. Most analyzed characters showed no differences between queens and workers. Such slight distinction is comparable to *Parachartergus smithii* (Mateus et al. 1997) and *Protopolybia exigua exigua* (Noll et al. 1996). Using log-log plots of the most discriminant characters (Fig. 8) and considering three distinct groups (queens, workers and intermediates), queens presented a type of allometric growth (Fig. 8A) comparable to *Epipona guerini* (Hunt et al. 1996) while workers and intermediates presented non-allometric growth. However, disregarding intermediates (as done by Jeanne 1996 in *Ps. difficilis*) and considering only two groups, i.e. individuals with or without ovary development (Fig. 8B), *Pseudopolybia vespiceps* presented only non-allometric growth and such pattern is quite similar to that found in *Ps. difficilis* (Jeanne 1996). Such a fact is very important because origin and role of intermediates relies primarily on their careful detection according to taxa and colony cycle.

In addition to diverse degrees of caste differentiation in this subfamily, the occurrence of intermediates, brought about complexity in the caste problems. Richards (1971) assumed that their role is the production of either trophic eggs or males but, Forsyth (1978), West-Eberhard (1978) and Gastreich et al. (1993) considered them as young uninseminated queens. Richards (1971) and West-Eberhard (1978) considered that, in a general way, intermediates have ovary development related to queen number. That is, in the presence of a few queens they present larger ovaries and vice-versa. Intermediates are present in species with low caste dimorphism (Richards, 1978; Noll et al., 1996; Mateus et al., 1997; present paper). On the other hand, species with pronounced caste dimorphism as *Agelaia vicina* (Sakagami et al. 1996), *A. pallipes* and *A. multipicta* (Noll et al. 1997) and *Apoica flavissima* (Shima et al. 1994) present sterile workers. However, uninseminated queens were found in *A. vicina* (Sakagami et al. 1996, Baio et al. in press.), *Polybia dimidiata* (Maule-Rodrigues & Santos 1974, Shima et al. 1996) and *Ro-*

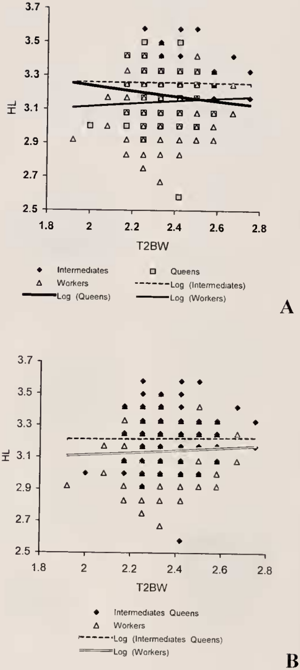

Fig. 8. Discrimination between queens, intermediates and workers of *Pseudopolybia vespiceps* using the log-log plots of basal width of tergite II (T_2BW) and head length (HL). A—Queens, workers and intermediates were separatedly plotted, B—Queens and intermediates were put together representing ovary-developed individuals and workers undeveloped-ovary individuals.

& Santos 1974, Shima et al. 1996) and *Ropalidia marginata* (Chandrashekara & Gadagkar 1991), and so their contribution to male production seems likely. In a general sense, intermediate females have been recorded in several other taxa, e.g., *Polybia chrysothorax, P. jurinei, Parachartergus fraternus* and *Angiopolybia* spp. (Richards and Richards 1951); *Brachygastra scutellaris* (Carpenter and Ross 1984), *B. lecheguana* (Machado et al. 1988). But, most of these species must be reanalyzed with a standardized statistical method. Richards (1971, 1978) mentioned that the intermediates characterize taxa in which structural caste differences are absent. This is, however, only partly valid, because *P. dimidiata* (Shima et al. 1996a) albeit characterized by clear cut caste dimorphism with queens smaller than workers, have intermediates also. In addition, Naumann (1970) and Simões (1977) and M. V. Baio (unpubl.) discovered their occurrence in two taxa, *Protopolybia acutiscutis* (cited as *P. pumila*) and *P. exigua*, which bear quite clear intercaste morphological differences. The latter observations are very important because in both cases the eggs laid by the intermediates were invariably eaten by nearby mates, which suggests likely importance in colony socio-economics, and remarkable similarities to the system of worker's trophic eggs widespread in the stingless bees (Zucchi 1993 and ref. therein). By using basic and multivariate statistics, the present study revealed another important facet about intermediates. It is noteworthy that conspicuous morphometric differences between queens and workers were not detected in *Pseudopolybia vespiceps* whereas intermediates tended to be larger (significantly larger in some characters, such as HW and PW) than queens and workers. Such trend was also suggested by distribution of plots on CAN_1 and CAN_2 axes (Fig. 4) and Mahalanobis distances (1.51 for Q/I vs. 0.99 for Q/W). In contrast, intermediates were more similar to queens in gaster color than to workers (Fig. 5–7), while similar to workers in head color and mesoscutellar spots of the mesoscutellum.

Another interesting fact refers to head form since most intermediates had flattened head or queen-unlike head (Fig. 5), as also suggested by the significant differences in HW. Intermediates were also different in ovaries which were shorter and had eggs smaller than those in queens (Figs. 2, 3). As relative age estimated by wing-wear was apparently not related to ovarian development (Fig. 3), it may suggest that long ovaries did not develop from shorter ones. Indeed, older females (Fig. 3) presented both ovary lengths. So, intermediates are apparently uninseminated specialized females that have invariably shorter but developed ovaries. There is a possibility that their eggs are trophic, and invariably eaten as in the afore mentioned *Protopolybia* species. In addition, they generally bear more abundant fat tissue than typical workers, and in some instances they may present as much fat tissue as true queens (Fig. 3, IV).

Colonies with intermediate females show curious combination of differences and similarities among the three types of females. These are probably related to the degree of caste differentiation: (1) species with intermediates more similar to workers usualy have clear-cut caste dimorphism (*Protopolybia exigua*, Simões 1977; *P. pumila* (= *acutiscutis*), Richards 1978; Naumann 1970); *P. sedula, Agelaia lobipleura melanogaster*, Richards 1978 and *Polybia emaciata*, Hebling and Letizio 1973); (2) species with intermediates more similar to queens have castes distinct in some characteristics (*Brachygastra bilineolata, Pseudopolybia compressa* morph *laticincta*, Richards 1978) or present clear-cut size dimorphism (*P. dimidiata*: Shima et al. 1996a) and (3) species with intermediates distinct in some characters can bear slight or no caste differences (*Pseudopolybia vespiceps*, present results, and *Belonogaster junceus*, Richards 1969) in which intermediates differed significantly from both castes in hamulus number (similar to *P. vespiceps*) and wing length, suggesting that these females are not merely queens or even ovary-developed workers (Richards, 1969).

In the studied case it is possible to consider intermediates by two ways: 1) Intermediates as young or uninseminated queens as pointed out by Forsyth (1978), West-Eberhard (1978) and Gastreich et al. (1993). In this case the pattern (Fig. 8B) is similar to that found in *Ps. difficilis* (Jeanne, 1996). 2) Specialized workers having a combination of queen and worker characters. In this case, intermediates have non-allometric growth but, queens presented allometric growth (Fig. 8A).

The present example shows how the caste system in neotropical swarm-founding polistine is complex and diverse. Moreover, the occurrence of intermediates in several polistine taxa turn the understanding of their social systems fascinating. The results at our hands suggest that the intermediates represent a specialized state. However, in the lack of substantial data a final conclusion has to be postponed.

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